STUDIES ON THE POPULATION DYNAMICS OF A THISTLE-FEEDING LADY BEETLE, *HENOSEPILACHNA PUSTULOSA* (KÔNO) IN A COOL TEMPERATE CLIMAX FOREST
II. LIFE TABLES, KEY-FACTOR ANALYSIS, AND DETECTION OF REGULATORY MECHANISMS

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INTRODUCTION

From 1974 to 1977, an intensive field study was carried out on the population dynamics of a thistle-feeding lady beetle, *Henosepilachna pustulosa* (KÔNO) (called *Hp* in this article) that was a denizen of a cool temperate climax forest. We executed an intensive marking, release and recapture program to investigate the population parameters and dispersal behavior of adult beetles. As outlined in the first paper of the series (NAKAMURA and OHGUSHI, 1979), the distinctive characteristics of *Hp* population were revealed as follows: reproductive rate (R), i. e., the ratio of the number of newly emerged adults in a given generation to that of overwintered adults in the preceding generation, was very small, ranging from 1-3, whereas winter survival was $>50\%$. Consequently, the size of population in the study area remained fairly constant at a relatively low density level when compared with the allied species, *H. vigintioctopunctata* (FABRICIUS) and *H. vigintioctomaculata* (MOTSCHULSKY), serious pests of the potato (abbreviated theses as *Hvp* and *Hvm*, respectively).

In this article, we have constructed the life tables to assess the components of mortality and to evaluate their effects on the variation in reproductive rate. To know what factor(s) are most responsible for regulating *Hp* population at a fairly stable level below the limit of food supply, we carried out the key-factor analysis on the life table and examined density relationships in the mortality and reproductive processes.

STUDY AREA AND METHOD

The study was carried out in the School Forest of Kyoto University at Asiu, 100 km north of Kyoto city. The Kamitani study area is rather flat and at an altitude of about 700 m and covered with cool temperate climax forest with *Fagus crenata* (BLUME) and *Quercus mongolica* (FISCHER) var. *grosseserrata* (REHDER et WILSON), etc. In Asiu adults and larvae of *Hp* feed on the leaves of the thistle, *Cirsium kagamontanum* (NAKAI), a perennial herb. The thistles grow in discrete units of
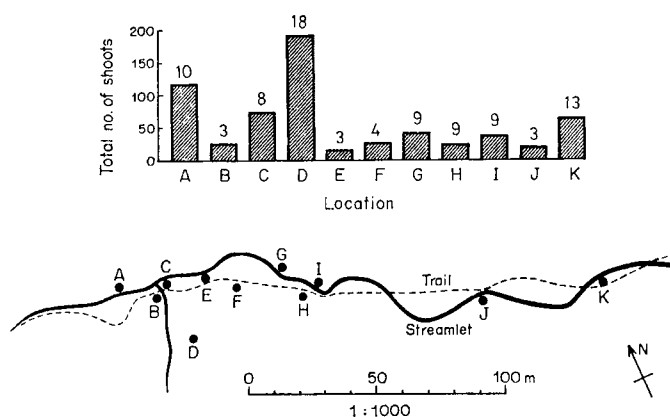
Fig. 1. Enlarged map of the Mondori subarea, showing the location and size of thistle patches. Letters refer to the names of patches. The height of histogram is proportional to the number of shoots growing on each patch (numeral on the histogram shows the number of thistle plants).

different size along a stream. Such an aggregation of thistles is referred to as a "patch" in this article. There are several aggregation of patches in the Kamitani study area, so that the study area could be split up into several "subareas", each of which contained a cluster of patches. A sketch map of the Kamitani area was presented in the previous paper (NAKAMURA and OHGUSHI, 1979). The Mondori subarea, which contained 11 thistle patches, was selected for the main study site and all the thistles were examined on each census (Fig. 1). The other subareas were also censused for comparative purposes.

1. *Laboratory works for estimating the fecundity, and developmental times in the immature stages*

Experiment 1: The overwintered adults collected from the Kamitani area were taken into the Chojidani Field Station, located in the east end of the Kamitani, and 20 pairs were isolated in plastic ice-cream cups (11 cm diameter and 8 cm depth) containing fresh thistle leaves. Each cup was examined daily (with some exceptions) for keeping a record of oviposition.

Experiment 2: Egg masses deposited in the cups were isolated in the new cups and records were kept of the hatching of eggs and the instar transitions. These observations were carried out at room temperature, synchronized with the process of field population.

2. *Estimation of numbers and mortality in the immature stages of Hp population in the field*

The routine censuses for construction of life tables were carried out from mid May to early October every third or fourth day in 1974, and once a week in 1975 and 1976. On each census all the thistles in the Mondori subarea were inspected.

Eggs: Eggs were laid in batches on the undersurface of host plants. All egg-masses were counted and thereafter labelled to prevent double counting. They were followed in successive censuses. The total number of eggs laid was obtained by assembling these data. The number of eggs hatched was assessed by counting the empty shells which were still present after hatching. Egg masses cannibalized by adults were recognized by the basal parts of the chorions remaining on the leaves. Eggs attacked by predators, such as earwigs and ground beetles were distinguished from eggs destroyed by other causes by the characteristic traces. We frequently observed that newly hatched larvae were cannibalizing eggs in the same mass. Early instar larvae also cannibalized the eggs. At times, unfortunately we could not clearly discriminate the eggs cannibalized by adults from those attacked by predators through the remaining traces. Moreover, eggs cannibalized by larvae could not easily be distinguished by the traces alone. Therefore the eggs were not included in the mortalities due to cannibalism (or predation) unless the eggs were observed being eaten or characteristic traces of cannibalism (or predation) were left after being attacked. Consequently, the percentage of egg mortalities due to cannibalism and predation were more or less underestimated. In the life tables, "failure to hatch" refers to the eggs which remained unhatched and shrivelled up.

Predator exclusion experiment with sticky barriers: In June of 1975, a field experiment was carried out to evaluate the impact of predation on the eggs. The egg masses, which were found on the host plants, were each isolated by sticky bands around them. The importance of predators was confirmed by comparison of egg mortalities with and without sticky barriers. This experiment was set up not only in the Mondori subarea but also in other subareas in the Kamitani.

Larvae and pupae: The size of larvae in early instars was too small to be counted exactly, and hence only the fourth instar larvae were counted at each census. The fully grown larvae chiefly pupated on the undersurface of the thistle leaves. The numbers of fourth instar larvae and pupae at the medial age of their instars (N_i) were derived by S/L, where S is the area enclosed by the seasonal prevalence curve of ith instar and time axis (Fig. 2) and L is the mean duration of ith instar (SOUTHWOOD and JEPSON, 1962). Numbers of larvae and pupae attacked by parasitic wasps, *Pediobius foveolatus* (CROWFORD) (Proctotrupidae) and *Watanabeia afissae* (WATANABE) (Eulophidae) were assessed by direct count of corpses which became dark and remained on the host plants for some time after dying.

New adults: We tried to estimate the total number of newly emerged adults by direct counting of pupal exuviae. Regrettably it was proved that the estimates obtained in this way were largely underestimated. We carried out an intensive marking, release and recapture program throughout the seasons to estimate the total sum of overwintered and newly emerged beetles. Therefore the number of over-wintered and new adults presented in Table 1 are estimates of the total number of
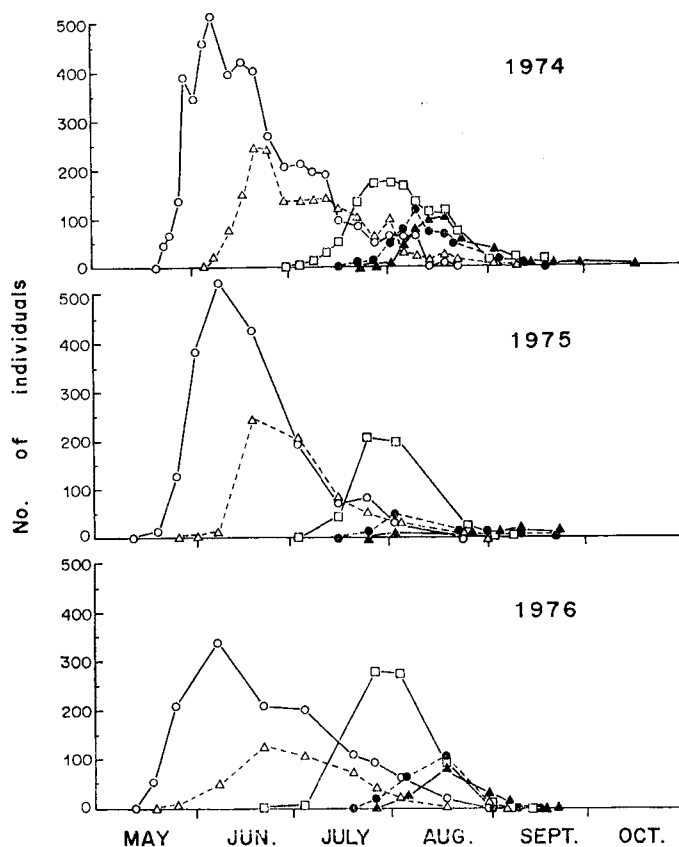
Fig. 2. Seasonal fluctuations in the number of individuals of each developmental stage of *H. pustulosa* in the Mondori subarea. (—○—) no. eggs laid per day, (--△--) no. eggs hatched per day, (—□—) no. 4th instar larvae, (--●--) no. pupae, (—▲—) no. adults emerged per day in ×10 scale.

adults emerged per season (N_G) derived by the JOLLY-SEBER method (SEBER, 1973) (For the details, see Table 2 in NAKAMURA and OHGUSHI, 1979).

RESULTS

1. *Seasonal fluctuations in numbers and developmental times of immature insects*

   Hp has one generation a year. Only a few days after the snow had melted in early May, post-hibernating adults began to emerge from hibernation site and appeared in the thistle patches. Seasonal fluctuations in numbers of immature insects are shown in Fig. 2. Experiment 2 shows that developmental times in each stage, assessed in the laboratory, were as follows; egg, 9 days; first instar, 10 days; second, 8 days; third, 10 days; fourth, 10 days; pupa, 7 days. Oviposition extended from late May to early August and a high peak was seen in early June. The new adults emerged from early August to early September and they entered hibernation before

Table 1. Life tables for *H. pustulosa* in the Mondori subarea from 1974 to 1976. Lx: ‰ survival in terms of eggs.

Age class	Causes of change in numbers	1974				1975				1976			
		No.	No. dying	% dying	LX	No.	No. dying	% dying	LX	No.	No. dying	% dying	LX
Overwintered adult		476	145 ♂♂ 331 ♀♀			459	159 ♂♂ 300 ♀♀			264	95 ♂♂ 169 ♀♀		
	Sex ratio (% ♀♀)	69.5				65.4				64.0			
	Fecundity (eggs/♀♀)	51.6				51.2				89.5			
Egg		17067			1000.0	15348			1000.0	15124			1000.0
	Cannibalism by adults		1158	6.8			405	2.6			262	1.7	
	Cannibalism by larvae		1409	8.3			335	2.2			964	6.4	
	Predation		1298	7.6			1612	10.5			1651	10.9	
	Failure to hatch		4755	27.9			1049	6.8			2923	19.3	
	Disappearence + unknown		2002	11.7			4979	32.4			3941	26.1	
	Total		10622	62.3			8380	54.5			9741	64.4	
L–hatched		6445			377.6	6968			454.0	5383			355.9
	Predation + unknown		5827	90.4			6464	92.8			4516	83.9	
L–4		618			35.2	504			32.8	867			57.3
	Parasites												
	W. afissae		18	2.9			5	1.0			22	2.5	
	P. fovoelatus		32*+10**	6.8			9+5	2.8			21+6	3.1	
	Unknown		—	—			87	17.3			—	—	
	Total		60	9.7			106	21.1			49	5.6	
New adult		560			32.8	398			25.9	865			57.2
		(209)***			(12.2)	(46)			(3.0)	(206)			(13.6)

*), **): No. of individuals parasitized in 4th instar and pupal stages, respectively.

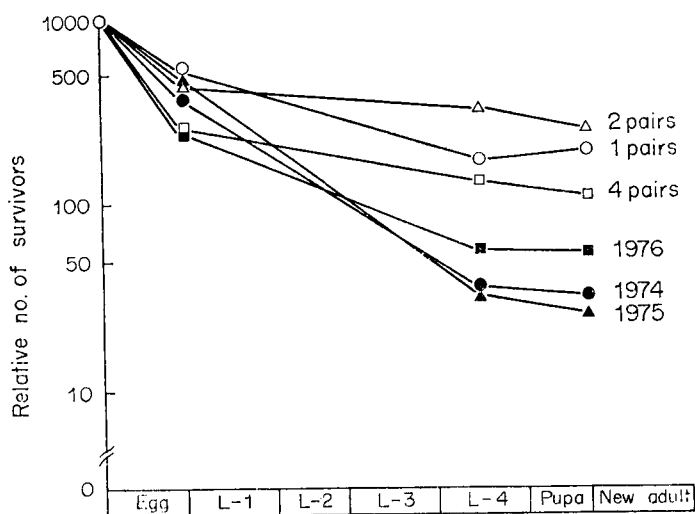***):Estimates based on the number of exuviae of pupa.

Fig. 3. Survivorship curves for *H. pustulosa*. Open and closed symbols indicate the caged and field populations, respectively. For details, see the text.

October (Seasonal changes in number of adults are presented in NAKAMURA and OHGUSHI, 1979).

2. *Life tables and population changes*

We constructed life tables for 1974-76 to summarize changes in Mondori subpopulation (Table 1). The survivorship curves from egg to adult emergence are shown in Fig. 3.

Before examining the factors causing changes in population size, the major changes that occurred are summarized as follows: in 1974, 476 beetles (331 ♀♀ and 145 ♂♂) emerged from hibernation site and appeared in the thistle patches and 17067 eggs were laid. These gave rise to 560 new adults (96.7% mortality). Among them 459 beetles (300 ♀♀ and 159 ♂♂) survived the winter and reappeared in the spring of 1975 and 15348 eggs were laid, which resulted in only 398 new adults (97.4% mortality). In the following spring (1976), 264 beetles (169 ♀♀ and 95 ♂♂) emerged after hibernation and laid 15124 eggs. From these eggs 865 beetles emerged in the autumn (94.3% mortality).

The reproductive rate, R, from 1974 to 1976 was 1.18 $(= \frac{560}{476})$, 0.87 $(= \frac{398}{459})$ and 3.28 $(= \frac{865}{264})$, respectively (NAKAMURA and OHGUSHI, 1979). The survival rate between autumn and the following spring (S_w) was 0.82 $(= \frac{459}{560}$, for 1974-75) and 0.66 $(= \frac{264}{398}$, for 1975-76). The smallest R in 1975 was mainly due to a heavy rain in late August, when about one third of the thistle colonies were flooded. The number of overwintered beetles was smallest in 1976, whereas the number of eggs laid per female and R were largest in that year. The fecundity and reproductive
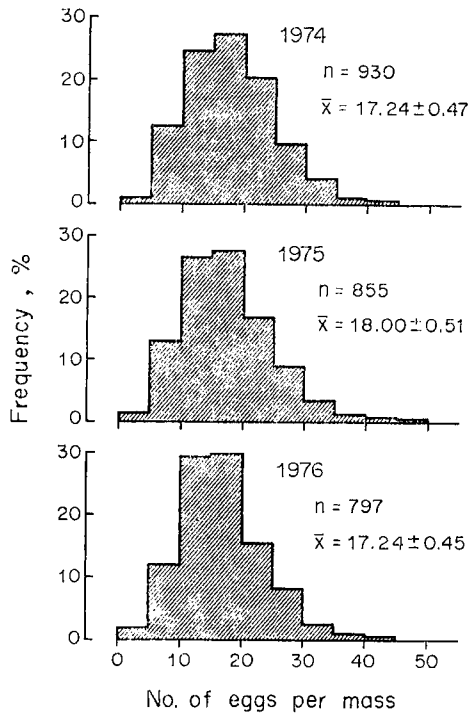
Fig. 4. Frequency distribution in the size of egg masses of *H. pustulosa*. The number of masses examined (n) and values of mean (x̄) with 95% confidence limits are given in the figure.

rate could be dependent on the density of overwintered adults. This relationship will be analysed in detail in later sections.

3. *Factors determining population size*

(1) *Adult fecundity*

The mean size of egg masses was 17-18 (Fig. 4), indicating that it was smaller than those of the two allied pest species, i. e., 28 for *Hvm* (IWAO, 1971) and 39 for *Hvp* (NAKAMURA, 1976a).

The result of experiment 1 shows that the mean number of eggs laid per female reared in the ice-cream cup was 155.7 (average of 20 iterations and at maximum 192).

No direct measurement of the fecundity was practicable in the field, but it was assessed indirectly as follows:

$$\text{Mean fecundity} = \frac{\text{Total no. of eggs laid in the Mondori subarea}}{\text{Total no. of overwintered resident females in the Mondori subarea}}$$

Since eggs were counted by successive thorough search of all the host plants and adult population was virtually self-contained in the Mondori subarea, the estimated values would be reasonable in accuracy. Mean fecundities thus obtained from 1974 to 1976

were: 51.6 ($=$17067/331), 51.2 ($=$15348/300) and 89.5 ($=$15124/169), respectively. The comparable information so far available is: nearly 500 in *Hvp* (NAKAMURA, 1976a) and more than 200 in H*vm* (IWAO, personal communication). From these data we can conclude that the mean fecundity of *Hp* population is much smaller in contrast to those of *Hvp* and *Hvm*. The potential fecundity of the Asiu population revealed by the field cage experiment (114.3, NAKAMURA in preparation) and rearing in the ice-cream cups (155.7) was much smaller than those of *Hvm* (700, IWAO, 1971) and *Hvp* (588, NAKAMURA, 1976b).

(2) *Egg mortality*

Mortality during egg stage was 62.3 (1974), 54.5 (1975) and 64.4% (1976), respectively.

(a) *Cannibalism by adult beetles*: More than thirty cases a year of adult beetles eating the egg masses were observed in the course of routine census. Cannibalistic tendency was more pronounced in female beetles than in male; in fact, 31 out of 34 cannibalizing beetles which were checked for sex were female beetles. Adult beetles were seen eating eggs even when adults and/or egg masses on the host plant were at a low density level. In many cases cannibalism occurred when there was only one adult and one egg mass on a thistle plant, indicating that no clear density relationships could be found in the egg cannibalism by adult beetles in the field population. The precentage of eggs cannibalized by adults was only 6.8% (1974), 2.6% (1975) and 1.7% (1976).

(b) *Cannibalism by larvae*: Only 2.2% (1975) to 8.3% (1974) of eggs were assessed to have been cannibalized by larvae. The percentage of eggs cannibalized by adults and larvae was evidently underestimated as mentioned earlier. The detailed analysis of cannibalizing behaviour of adult beetles and its ecological consequences are interesting and need to be studied.

(c) *Predation*: The predators, which were found to be feeding on eggs, have been identified as follows: an earwig, *Anechura harmandi harmandi* (SAKAI), a staphilinid, *Paederus poweri* (SHARP) and two species of ground beetles, *Platynus ehikoensis* (HABU) and *P. elainus* (BATES). Among them, *A. harmandi harmandi* seemed to be most important as an egg predator. Many earwigs, often more than ten at the peak, were seen roaming about on a thistle plant, and they were the most dominant predator on the thistle plants. Although earwigs were found only in a restricted period, their activity coincided in time with the high peak of oviposition of *Hp*.

This list of predators is by no means exhaustive, since no systematic search for predators was made in this study. Besides the species recorded above, many arthropods, such as spiders, mites, and ants were found in large numbers on the thistles

and they were suspected as egg predators.

The results of the predator exclusion experiments are summarized as follows:

Treatment	with barriers
Total no. of eggs examined	1045
No. of egg masses (mean size)	50 (20. 9)
Total no. of eggs hatched (%)	885 (84. 7%)

When predators were excluded the percentage of eggs hatched increased to 84. 7%, compared with only 35. 6-45. 5% without barriers, as shown in Table 1. This reveals clearly that eggs of *Hp* were subjected to severe arthropod predation.

(d)*Failure to hatch*: Egg mortality due to failure to hatch varied 27. 9, 6. 8 and 19. 3% from 1974 to 1976, respectively. Judging from the fact that nearly all of the eggs that were taken into the laboratory hatched before mid June, egg mortality due to infertility might be negligible in the early oviposition period. Whereas most eggs which were oviposited from mid June onward soon became dark and shrivelled up, but whether this was caused by sterility or high temperature was not examined.

(3) *Larval and pupal mortality*

As shown in Fig. 3, the mortality rate was higher during the early instars (from first to third instar) than during the later stages (from fourth instar to pupa). However, there are two reasons to believe that the number of fourth instar larvae assessed by the equation S/L (presented in Table 1) was apparently underestimated. This is in part due to the fact that the temperature in the field was somewhat higher than that in the room, so that the duration of the fourth instar stage in the field might be a few days shorter than the estimate obtained at room temperature (Experiment 2), and in part to the fact that a small proportion of fourth instar larvae tended to wander from thistles and pupate on the neighbouring plants. Except for death from parasitism, the actual causes of larval mortality were difficult to work out because we rarely found larvae being attacked or remains of dead individuals.

A parasitic wasp, *Watanabeia afissae* emerged from only fourth instar larvae in the first half of August, whereas the other wasp, *Pediobius foveolatus* bred mainly from fourth instar larvae and partially from third instar larvae and pupae. *P. foveolatus* emerged in late August and September. The number of adult wasps developed in a single host larva was only one for *W. afissae* and varied from one to more than ten for *P. foveolatus*, respectively. The extent of parasitism by both *W. afissae* and *P. foveolatus* made up a small percentage of the total number of fourth instar larvae and pupae (9. 7, 3. 8 and 5. 6% from 1974 to 1976, respectively). At the present it is improbable that *Hp* population was seriously affected by parasitism.

In the field cage experiment where all the predators were excluded the larvae depleted the food plant to such an extent that starvation had a marked effect on larval mortality, however the mortality for the period from egg hatching to adult emergence was only 50% (NAKAMURA in preparation). Food depletion rarely occurred in the field population during the study period, but larval mortality was much higher, ranging from 84 to 95%, than that for the caged population. These lines of circumstantial evidence would further confirm that larval mortality, particularly during the early instars, was mainly attributed to arthropod predation. Egg predators such as earwigs, spiders, and groundbeetles are also regarded as possible predators to early instar larvae.

(4) *Analysis of life table data*

1. *Key factar analysis*

In the examination of life table data, VARLEY and GRADWELL's (1960) graphical method of key-factor analysis was used to evaluate the contribution of each separate mortality to overall mortality.

The index of population trend (I) and the reproductive rate (R) are expressed as follows:

$$R = \frac{E}{A_0} \times \frac{L_1}{E} \times \frac{L_2}{L_1} \times \frac{A_E}{L_2} = \frac{A_E}{A_0}$$

$$I = R \times \frac{A_S}{A_E} = \frac{A_S}{A_0}$$

where A_0 (and A_S) = number of overwintered females in the spring of i year (and $i+1$ year), E = total number of eggs laid, L_1 = number of eggs hatched, L_2 = number of 4th instar larvae, A_E = number of newly emerged females in the autumn of i year. The index of population trend (I) may be expressed as the product of the fecundity and survival rates:

$$I = E_F \times S_E \times S_{L1} \times S_{L2} \times P_W$$

Taking logarithms,

$$\log I = \log R + \log P_W$$
$$= \log E_F + \log S_E + \log S_{L1} + \text{Log } S_{L2} + \log P_W$$

where E_F, the fecundity index which is a suitable measure for the number of eggs laid per female, S_E, survival of eggs, S_{L1}, survival from 1st to 4th instar larvae, S_{L2}, survival from 4th instar to adult emergence, $P_W (= A_S/A_L)$, the rate of population change in the adult numbers for the period from autumn to the following spring. P_W is almost synonymous with the survival rate of adult beetles between autumn and the following spring, if it is calculated for the total population in the Mondori subarea, (Fig. 6d). However if P_W is measured for the individual patch it is affected by the degree of inter-patch dispersal by adult beetles after hibernation, as well as by the mortality during winter (for details, see NAKAMURA and OHGUSHI, in

preparation). Since the number of beetles on each patch was too small to apply JOLLY's formula directly, the population sizes of female beetles (A_O, A_E and A_S) were estimated by the average number of beetles per census on or near the days when they were at the maximum. The values obtained were not corrected by sex ratio, for the sex ratio of beetles on each patch did not deviate greatly from the average. Since A_O does not denote absolute numbers but relative values, E_F provides an index of fecundity. The changes in numbers in six successive phases of lifecycle (from
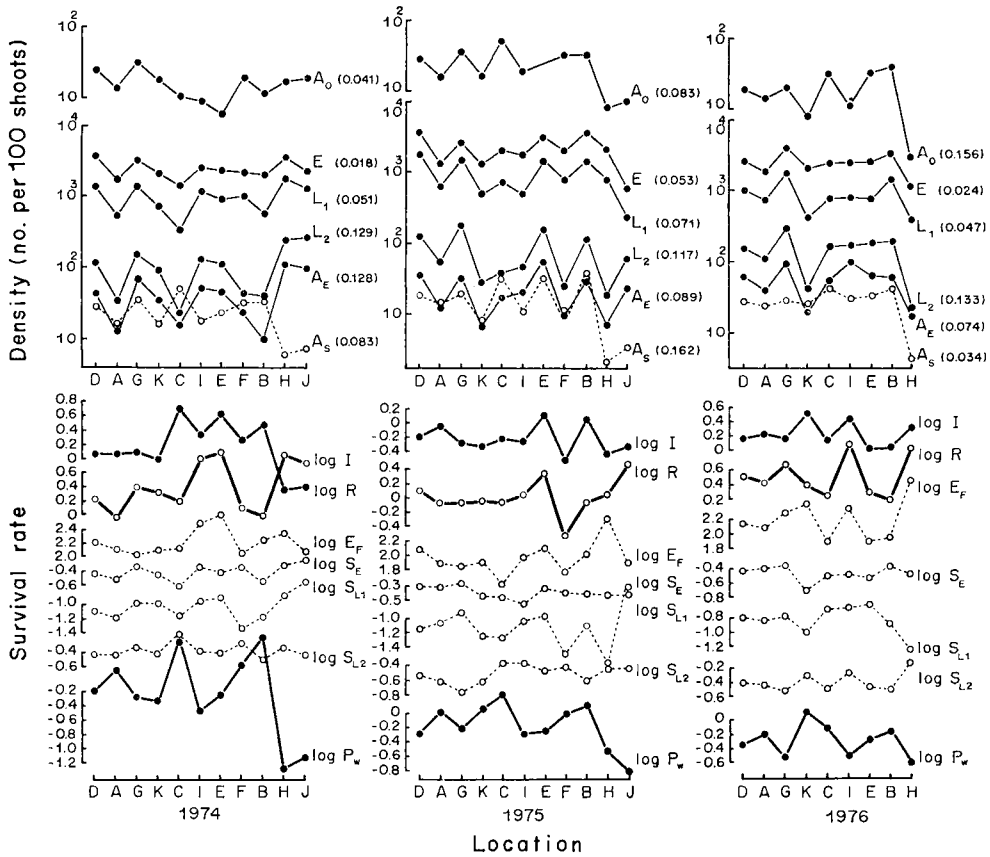
Fig. 5. Comparison of changes in density and survival rate among different thistle patches for the period from overwintered adults, through hibernation, to the overwintered adults the following spring.

Upper:density change. A_O=overwintered adults; E=eggslaid; L_1=eggs hatches; L_2=4th instar larvae; A_E=adults emerged; A_S=overwintered adults the following spring.

Lower: changes on survival rate. I=trend index; R=reproductive rate; E_F=fecundity index; S_E=percentage of eggs hatched; S_{L1}=survival rate from 1st to 4th instar; S_{L2}=survival rate from 4th instar to adult emergence; P_W=the population change for the period between autumn and the following spring. Values in parentheses indicate the variance of the density in logarithm amongpatches. For details, see the text.

A_o to A_s) are plotted against different patches (Fig. 5, upper) or different years (Fig. 6, upper). The variance of the logarithms of numbers (or density) is calculated for each life stage to know at what stage the variation is imposed or the regulation exerted. Then, the recognition of the key-factor for variation in I or R is done by visual correlation on the graphs (Fig. 5 and 6, lower).

   (a) *The key-factor causing the variation of I or R among different patches*: Since the size of thistle patches varied widely, all the population estimates were converted to the numbers per 100 shoots of host plants. The variances were reduced significantly from overwintered adult to egg, and minimal variation occurred in the egg stage (Fig. 5, upper). This reduction suggests that there might be some density-regulating mechanism operating on each patch in the ovipositing process. Thereafter the variance increased rapidly from hatched egg to the new adults.
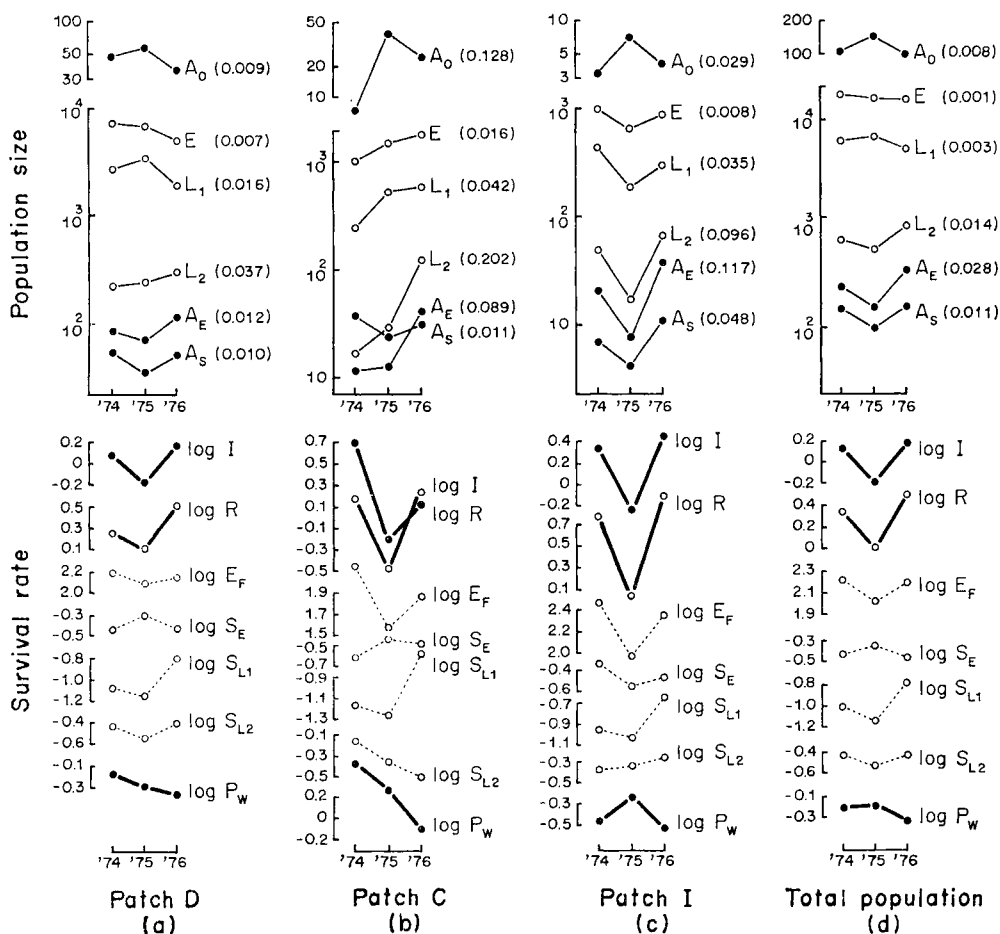

Fig. 6. Comparison of changes in numbers and survival rate on an individual patch (a-c) and the total population in the Mondori subarea (d). The patches D, C and I are largest, intermediate and small in size, respectively. See explanation of Fig. 5.

However the following spring the variance of overwintered adults was reduced again below that of before hibernation. Moreover patches with higher adult density in the autumn tended to become less crowded the following spring, and *vice versa*. This conclusion can be applied to the generation during autumn of 1975 and the following spring of 1976, if patches J and H which were so small in size and/or poor in quality as to be affected by chance are excluded in the analysis. This evening out of the population could have resulted from a density-related redistribution of overwintered adults among patches, as shown later (Fig. 7). From the graphs we can conclude that, first, E_F which refers to the number of eggs laid per female was the key-factor causing the variation of R among patches, secondly, log P_W ran counter to changes in log R, indicating that adult dispersal tended to compensate for variations in reproductive rate (R), and to reduce the variability of I.

(b) *The key-factor causing the annual fluctuation in I and R*: The key factor analysis was applied to an individual patch (Fig. 6a-c) and to the total population in the Mondori (Fig. 6d). In Fig. 6d, the average numbers of adult beetles per census on or near the days when they were at the maximum (Table 5 in NAKAMURA and OHGUSHI, 1979) were used for A_O, A_E and A_S, because censuses in 1977 were carried out only three times in both spring and early autumn, so that the total number of adult beetles emerged in 1977 could not be estimated by the JOLLY's method. Variance on patch D was relatively small at every stage and it was not reduced significantly from overwintered adult (A_O) to egg (E). On patch D, the reduction in fecundity (E_F) was not strongly correlated with log I and log R. This is probably due to the fact that patch D was large enough to contain a high degree of heterogeneity. However, the variances of most of the smaller patches were reduced more clearly from A_O to E and from A_E to A_S, and log E_F was strongly correlated with log I and log R (patch C and I were taken for examples in Fig. 6b-c). It is very impressive that there was very small variance in the egg stage of the total population in the Mondori subarea. This was brought about by the fact that the number of overwintered adults was smallest in 1976, whereas the number of eggs laid per female was largest in that year (Table 1). The conclusions drawn from Fig. 5 can be applied generally to Fig. 6.

2. *Analysis of regulatory processes*

To make clear possible density-dependence in the inter-patch dispersal and egg laying processes by overwintered adults, the relationships between A_E and P_W (Fig. 7) and between A_O and E_F (Fig. 8) were examined. Since the amount of food plants on each patch remained nearly constant during the four-year study period, the relationships could be detected by using the adult numbers (A_E or A_O) for each patch (Figs. 7 and 8, left graphs). Thereafter, we inspected the density-dependent relationships among the patches of various sizes all together by converting the adult numbers into the density in terms of 100 shoots of host plants (Figs. 7 and 8, right
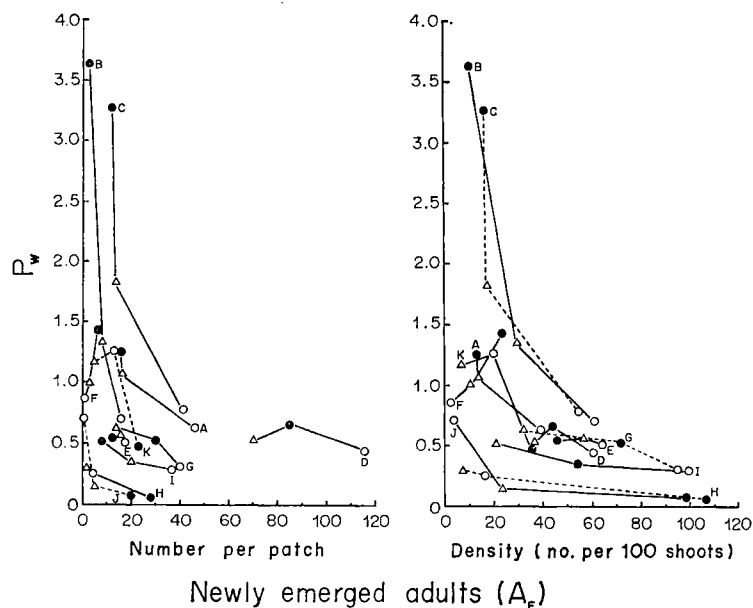
Fig. 7. Relationship between the number (left figure) or the density (right figure) of new adults and P_W, the population change for the period between autumn and the following spring. Letters refer to the patches. ●, △ and ○ indicate the generations for 1974-75, 1975-76 and 1976-77, respectively.
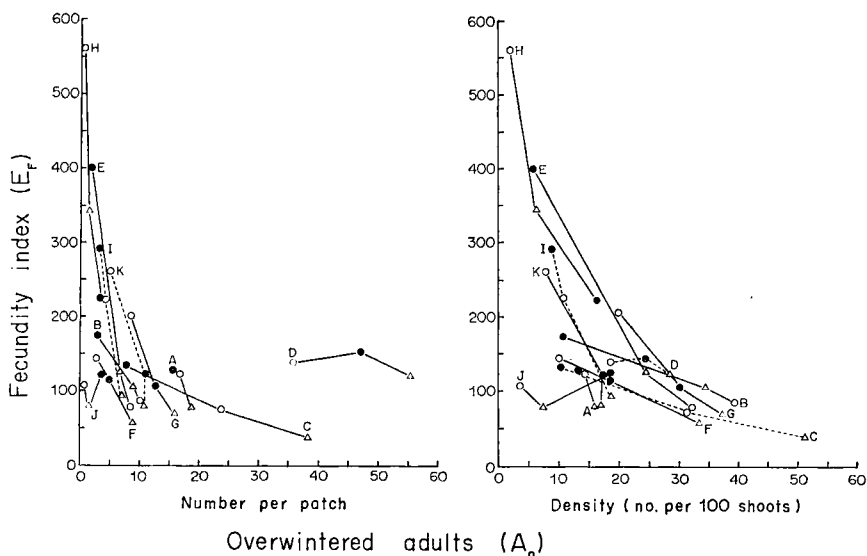

Fig. 8. Relationship between the number (left figure) or the density (right figure) of overwintered beetles and the fecundity index, E_F. Letters refer to patches. ●=1974; △=1975; ○=1976.

graphs).

Fig. 7 shows that P_W, the population change in the adult numbers between pre- and post-hibernating period, was strongly density-dependent. This was mainly due to inter-patch dispersal of overwintered adults, rather than to mortality before or during winter. The reasons are: (1) during the pre-hibernation period the survival rate of new adults was very high (>0.96 per day, NAKAMURA and OHGUSHI, 1979) and new adults were extremely sedentary and remaining in the same patch where they had emerged until they entered hibernation, and (2) on each patch the survival rate during winter was very high ($\gg 0.5$) and no simple relationship was found between the density of new adults and the survival rate during winter. The dispersal behaviour of adult beetles will be presented in detail in the following paper.

Fig. 8 indicates the relationship between the density of overwintered adults on each patch (A_O) and the fecundity index (E_F), showing that fecundity sharply decreased in a density-dependent manner. Density-dependent reduction in the fecundity was not detected on patches D and J, because D was the patch of the greatest size and contained a high degree of heterogeneity, and J was the smallest size and very poor in quality (Fig. 8).

Egg mortality, survival from first instar to fourth instar and survival from fourth instar to adult emergence did not show any clear tendencies for density-dependence (Fig. 9). Therefore arthropod predation might not have been a simple case of density-dependent regulation.

R was derived by multiplying fecundity (E_F) by survival rate from egg to adult emergence (S_E, S_{L1}, and S_{L2} in Fig. 9). Since E_F was strongly dependent on the adult density (A_O), R was also dependent on A_O, however the plots are widely scattered probably due not only to density-independent variations in the mortality from egg to adult emergence but also to the heterogeneity in the quality of patches (Fig. 10).
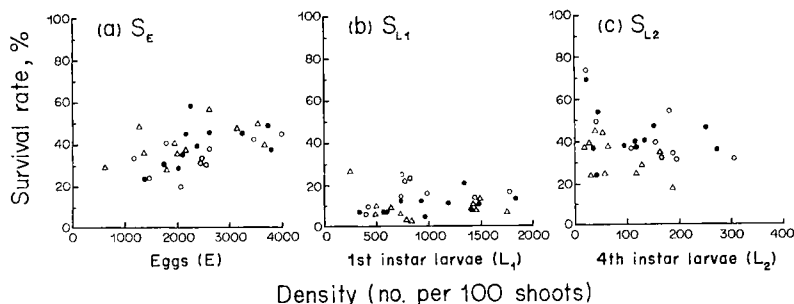

Fig. 9. (a) Relationship between the density of eggs and the percentage of eggs hatched (S_E); (b) relationship between the density of eggs hatched and the survival rate to the 4th instar (S_{L1}); (c) relationship between the density of 4th instar larvae and survival rate to adult emergence (S_{L2}). ●=1974; △=1975; ○=1976.
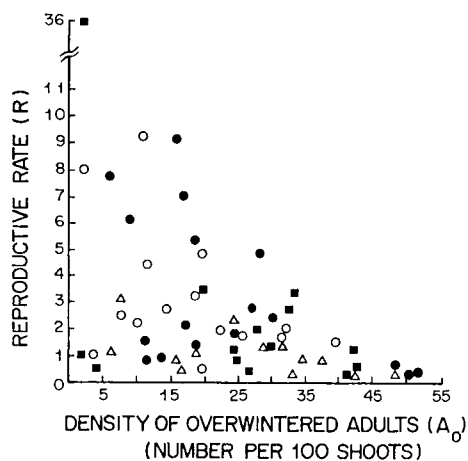
Fig. 10. Relationship between the reproductive rate, R, and the density of overwintered adults on each patch. ●=1974; △=1975; ○=1976; ■=1977.

DISCUSSION

Inter-patch dispersal of adult beetles as a regulating factor: Results of key-factor analysis indicated that the stabilization of population size was attained through density-dependent regulatory processes operating in inter-patch dispersal and in oviposition by overwintered adults (Figs. 5 and 6). We traced the movement path of marked beetles to show the movement patterns of adult beetles in different levels of habitat units (NAKAMURA and OHGUSHI, in preparation). The results indicate that, although the subpopulation in the Mondori was nearly self-contained, inter-patch movements of overwintered adults were so frequent that the patches in the Mondori were closely connected with each other. The movement patterns of overwintered adults consisted of short-distance diffusions. However, new adults were extremely sedentary, remaining in the same patch where they had emerged until they entered hibernation. A few days after the snow had melted, the overwintered adults emerged from hibernation site and appeared in the thistle patches almost simultaneously. At that time, the thistles were in small rosette form, so that the amount of mutual contact between individuals was very high, resulting in a higher level of dispersal activity than that found in a later period when thistles were larger. Thus the following processes were involved: firstly, the exodus and interchange of overwintered beetles among patches occurred density-dependently, which led to reduced variation in density among patches. Secondly, density-dependent regulation of fecundity on each patch could be mainly attributed to density-induced adult dispersal rather than to direct effect of overcrowding, because the increased degree of mutual contact among overwintered beetles would cause the increased dispersal tendency and limit the time available for egg laying.

As mentioned earlier, the total number of overwintered beetles emerged in the Mondori subarea was smallest in 1976, whereas the fecundity of overwintered beetles was by far larger in 1976 (89. 5) than those in 1974 (51. 6) and 1975 (51. 2). This suggests that the density-dependent regulation in fecundity would be exerted also in larger spatial scale (the whole Mondori subarea) as well as in smaller scale (each individual patch). NAKAMURA and OHGUSHI (in preparation) indicated that the dispersal activity of overwintered beetles, in 1976 was about one third as compared with those of 1974 and 1975. While, the longevity of overwintered adults was much longer in 1976 (50 < days) than those in 1974 (30 days) and 1975 (40 days) (NAKAMURA and OHGUSHI, 1979). They concluded that the larger fecundity attained in1976in the whole Mondori subarea would be not only due to the longer life span adult, but also due to the density-dependent decrease in dispersal activity. The dispersal behaviour and spatial dynamics of the Asiu population will be presented in the subsequent paper (NAKAMURA and OHGUSHI, in preparation).

Arthropod predation as a conditioning factor: In Asiu, arthropod predation, which caused a high mortality in egg and larval stages, might not have been a simple case of density-dependent regulation (Fig. 9). But it might have operated as a conditioning factor which determined the density level of *Hp* population below the food ceiling. This could be deduced from the recent work of OHGUSHI and SAWADA (in preparation). They have been studying several local populations in Shiga Prefecture, 10-15 km east of Asiu, in order to compare demographic characteristics among them. They found that a local population at Nyudani frequently defoliated the food resources mainly due to low intensity of predation. They concluded that the variance of *R* among different habitats was largely dependent on the magnitude of predatory pressure. Accordingly, in Asiu the fluctuations of population size were stabilized under the strong influence of density-dependent processes during the oviposition period, but without extensive mortality due to arthropod predation this process alone probably would not prevent the *Hp* population from reaching such a high density as attained in the Nyudani population. There have been some field studies to show that predators (mainly polyphagous) play an important role in limiting the density of insect populations to a low level (e. g., DEMPSTER 1971: EICKWORT, 1977; FURUTA, 1976). Further studies are needed to reveal in more detail the nature of the interaction between the *Hp* population and the various species of predators.

Density level at which Asiu population is regulated: The degree of mutual contact among overwintered adults appeared to be rather high when thistles were in the small rosette stage. But the impact of feeding by overwintered adults and early-instar larvae on the food plants was slight, due mainly to the rapid growth of thistles. The feeding damage caused by later-instar larvae and newly-emerged adults was somewhat more noticeable, but even these heavier feeders did not deplete the

thistles enough to starve. Although it is usually difficult to estimate the amount of food resources quantitatively and to know the fraction of food consumed in field studies, in those observations, fourth-instar larvae and new adult did not appear to consume more than half of the leaves available. However, the remaining leaves were heavily stained with the excrement of larvae and new adults. Such contamination might effectively increase the degree of crowding on a thistle leaf far beyond that to be expected from defoliation alone. Accordingly, the density of fourth-instar and new adults might well have reached a level just below the carrying capacity of the food plants.

Population characteristics of the Asiu population living under stable and permanent habitat condition: Table 2 summarizes the population characteristics of the Asiu population in comparison with those of the potato beetle (*Hvp*) which was studied in as much detail by NAKAMURA (1976a, b). The overwintered adult of *Hvp* was smaller in body size and much shorter in longevity than that of *Hp*, however the fecundity of *Hvp* was much higher than that of *Hp*. The *Hvp* population was subjected to low intensity of predation pressure during egg and larval period. Accordingly, the potato beetle had a much higher reproductive rate than that of the thistle beetle, ranging from 20 to 60, and frequently reached a density level where severe starvation occurred. For the potato beetle, a large value of *R* combined with strong power of dispersal is a proper reproductive strategy as a pest. On the contrary, the thistle beetle population in Asiu which lives in a permanent and stable habitat showed a low reproductive rate per generation with low fecundity and long adult life, and it maintained fairly constant in population size just below the food

Table 2. Comparison of demographic characteristics of the two allied species of phytophagous lady beetles, *Henosepilachna pustulosa* and *H. vigintiocto-punctata.* *

Characteristics	H. pustulosa	H. vigintioctopunctata
Habitat (Stability)	cool temperate climax forest (Stable and permanent)	cultivated fields (variable)
Body size	larger	smaller
Longevity of overwintered adults	40-60 days	15-20 days
Fecundity per female (potential)	50-90 (200-400?)	500 (600-1000?)
Dispersal of adults	sedentary	mobile
Mortality rate (egg–new adult)	98-99% (arthropod predation)	90% (starvation)
Reproductive rate, R	1-3	20-60
Density level	below the food limit, but not rare	enough high to deplete food resources
Fluctuation of population size	stabilized through density-dependent dispersal of adult beetles	violent fluctuation without effective regulation mechanism

*After NAKAMURA (1976a, b)

limit. According to the r-K continuum defined by SOUTHWOOD (1975, 1977), it can be said that Hp in Asiu is more K strategic than the two allied pest species (especially Hvp) or other pest species such as Colorado potato beetle, *Leptinotarsa decemlineata* (HARCOURT 1964, 1971; LATHEEF and HARCOURT 1974; KARG and TROJAN 1968).

Local populations of Hp are known to be considerably different in their morphological and ecological characteristics (KATAKURA, 1974a, b, 1977). The demographic attributes of some local populations are expected to be markedly different from those in Asiu. Particularly, the populations that live in unstable habitats (OHGUSHI and SAWADA, in preparation) and that feed on the potato (WATANABE and SUZUKI, 1965; YASUTOMI, 1976) and blue cohosh, *Caulophyllum robstum* (FUKUDA, 1970) are most interesting from the stand point of evolution of ecological strategies as well as population dynamics. Comparative studies on population dynamics of Hp populations have just begun, but certainly will be promising.

SUMMARY

From 1974 to 1977, a field study was carried out on the population dynamics of a thistle-feeding lady beetle, *H. pustulosa*, that was a denizen of a cool temperate climax forest in Kyoto Prefecture, Japan. The size of populations in the study area remained remarkably constant, and never reached a level where intensive intraspecific competition occurred. Life tables were constructed for three years (1974-76) to summarize changes in the popualtion. Adult fecundity varied from 51.2 to 89.5, but potential fecundity would be 200 or more. Mortality during the egg stage ranged from 54.5 to 64.4%, mainly due to arthropod predation. The chief predators included were earwig, *Anechura harmandi harmandi*, a staphilinid, *Paederus poweri*, and two species of ground beetles, *Platynus ehikoensis* and *P. elainus*. Among them, *A. harmandi harmandi* seemed to be most important as an egg predator. Egg mortality also included cannibalism by adults and larvae of *H. pustulosa*. The larval mortality from first to third instar was very high (83.9-92.8%) presumably mainly attributable to arthropod predators. The extent of parasitism by two wasps, *Watanabeia afissae* and *Pediobius foveolatus*, ranged from 3.8 to 9.7% of fourth instar larvae. Since feeding damage caused by larvae never reached a level where food plants were seriously depleted, mortality due to starvation rarely occurred during the study period. Results of key-factor analysis indicated that the stabilization of population size was attained through density-dependent regulatory processes operating in inter-patch dispersal and in oviposition by overwintered adults. The following processes were involved:

1. The exodus and interchange of overwintered beetles among patches occurred density-dependently, which led to reduced variation in density among patches.

2. Density-dependent regulation of fecundity on each patch could be mainly attributed to density-induced adult dispersal rather than to direct effects of overcrowd-

ing. Egg mortality, survival from first instar to fourth and survival from fourth instar to adult emergence did not show any clear tendencies for density-dependence. Therefore, arthropod predation might not have been a simple case of density-dependent regulation. It might have operated as a conditioning factor which determined the density level of *H. pustulosa* population. The *H. pustulosa* population in Asiu which lives in a permanent and stable habitat thus appears to be controlled mainly by the density-dependent regulatory processes mentioned above. The demographic characteristics of *H. pustulosa* was discussed in contrast to those of the allied potato beetle, *H. vigintioctopunctata.*

REFERENCES

DEMPSTER, P. J. (1971) The population ecology of the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera, Arctiidae). *Oecologia* 7: 26-67.

EICKWORT, K. R. (1977) Population dynamics of a relatively rare species of milkweed beetle (*Labidomera*). *Ecology* 58:527-537.

FUKUDA, A. (1970) An unrecorded form of the *Epilachna vigintioctomaculata* complex feeding on *Caulophyllum robustum* MAXIM. *Kontyû* 38: 348-352. (in Japanese with English summary)

FURUTA, K. (1976) Studies on the dynamics of the low density populations of Gypsy moth and Todo-fir aphid—analysis of the environmental resistance factors by artificial host increase method. *Bull. Gov. For. Exp. Sta. No.* 279:1-85. (in Japanese with English summary)

HARCOURT, D. G. (1964) Population dynamics of *Leptinotarsa decemlineata* (SAY) in eastern Ontario. II. Population and mortality estimation during six age intervals. *Can. Entomol.* 96: 1190-1198.

HARCOURT, D. G. (1971) Ditto. III. Major population processes. *Can. Entomol.* 103: 1049-1061.

IWAO, S. (1971) Dynamics of numbers of a phytophagous lady-beetle, *Epilachna vigintioctomaculata,* living in patchily distributed habitats. *Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970)* pp. 129-147.

JOLLY, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration—stochastic model. *Biometrika* 52: 225-247.

KARG, J. and P. TROJAN (1968) Fluctuations in numbers and reduction of the Colorado beetle (*Leptinotarsa decemlineata* SAY) in natural conditions. *Ekol. Polska Ser. A*, 14: 147-169.

KATAKURA, H. (1974a) Variation analysis of elytral maculation in *Henosepilachna vigintioctomaculata* complex (Coleoptera, Coccinellidae). *J. Fac. Sci. Hokkaido Univ., Ser. VI, Zool.* 19: 445-455.

KATAKURA, H. (1974b) Morphology and distribution of the forms of *Henosepilachna vigintioctomaculata*. *J. Fac. Sci. Hokkaido Univ., Ser. VI, Zool.* 19: 657-680.

KATAKURA, H. (1977) A review of *Henosepilachna vigintioctomaculata* complex, phytophagous lady beetles. *Insectarium* 14:80-87. (in Japanese)

LATHEEF, M. A. and D. C. HARCOURT (1973) A sampling plan for studies on the population dynamics of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) on tomato. *Ent. exp. & appl.* 16: 365-372.

NAKAMURA, K. (1976a) Studies on the population dynamics of the 28-spotted lady beetles, *Henosepilachna vigintioctopunctata* F. I. Analysis of life tables and mortality process in the field population. *Jap. J. Ecol.* 26: 49-59. (in Japanese with English summary)

NAKAMURA, K. (1976b) Ditto. II. Analysis of regulatory system under seminatural and laboratory conditions. *Jap. J. Ecol.* 26: 125-134. (in Japanese with English summary)

NAKAMURA, K. and T. OHGUSHI (1979) Studies on the population dynamics of a thistle-feeding lady beetle, *Henosepilachna pustulosa* (KÔNO) in a cool temperate climax forest. I. The estimation of adult population parameters by the marking, release and recapture method. *Res. Popul. Ecol.* 20: 297-314.

SEBER, G. A. F. (1973) *The estimation of animal abundance and related parameters*. Griffin, London.

SOUTHWOOD, T. R. E. (1975) The dynamics of insect populations. In: *Insects, Science and Society*. D. PIMENTEL (ed.) pp. 151-199.

SOUTHWOOD, T. R. E. (1977) Habitat, the templet for ecological strategies? *J. Anim. Ecol.* 46: 337-365.

SOUTHWOOD, T. R. E. and W. F. JEPSON (1962) Studies on the populations of *Ocinella frit* L. (Dipt: Chloropidae) in the oat crop. *J. Anim. Ecol.* 31: 481-495.

VARLEY, G. C. and G. R. GRADWELL (1960) Key factors in population studies. *J. Anim. Ecol.* 29: 399-401.

WATANABE, C. and S. SUZUKI (1965) A consideration of food preferences of the *Epilachna vigintioctomaculata* complex, with special reference to the so-called "Tokyo west suburbs form". *Kontyû* 33: 191-198. (in Japanese with English summary)

YASUTOMI, K. (1967) Notes on the geographical distribution and host preference in the Tokyo West-suburb form of *Epilachna vigintioctomaculata* complex. *Kontyû* 44: 111-114. (in Japanese with English summary)

ブナ原生林地帯に生息するコブオオニジュウヤホシテントウの個体群動態
II. 生命表と基本要因分析による個体数調節機構の検出

中 村 浩 二・大 串 隆 之

京都市の北方 100 km にある京大芦生演習林のブナ原生林の渓流ぞいにはえるカガノアザミを食するコブオオニジュウヤホシテントウを 1974 年から 1977 年にかけて調査した。調査期間を通じて本種はアザミを食いつくすような高密度に達することはなく，しかも安定した個体群サイズを維持していた。生命表を作製したところ，メス1匹あたりの野外での産卵数は 50〜90 個と推定され，これは近縁種で害虫であるニジュウヤホシテントウやオオニジュウヤホシテントウよりずっと少なかった。卵の死亡率は 55〜64%，ふ化から羽化までの幼虫期死亡率は 84〜94% であり，コブハサミムシやゴミムシなどによる捕食が重要な死亡要因であった。幼虫は2種の寄生蜂に攻撃されるが，寄生率はふ化した幼虫数の1%以下にすぎなかった。越冬成虫はパッチ状に分布しているアザミ群落を頻繁に移動，交流する。この過程は密度依存的におこるのでパッチごとの成虫密度が均一化されるとともに，産卵数の密度依存的調節もおこった。この越冬成虫の分散の過程が本種個体群の安定化にとって最も重要であることがわかった。越冬成虫は雪どけ直後に一斉に飛来するが，この時期にはアザミは小さなロゼットにすぎず食草上での混み合いが高くなり密度に依存した分散が生ずるのであろう。卵や幼虫に対する捕食は高い死亡率をもたらすが，密度依存性や Key-factor としての重要性は検出されておらず，本種個体群を低い密度レベルに抑える Conditioning factor として働いているものとみられる。またブナ原生林地帯の安定したハビタートに生息するこの個体群の動態の特性を近縁種で害虫であるニジュウヤホシテントウと比較して論じた。